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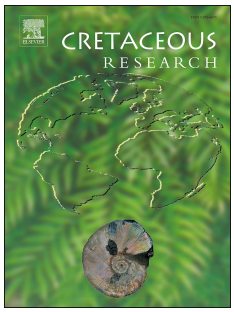

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Re-examination of the palynological content of the Lower Cretaceous deposits of Angeac, Charente, south-west France: age, palaeoenvironment and taxonomic determinations

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Abstract

Further to the work published by Néraudeau et al. six years ago, palynological matter recovered from the lignitic bone bed of Angeac in Charente (south-west France) has been re-examined in order to provide more evidence of its age, the previous Hauterivian–Barremian interpretation being regarded as controversial. The samples come from four sedimentological units, An2–An5, which together yielded an assemblage of 34 species, taxonomically dominated by palaeoecologically significant lygodiaceous verrucate spores, including eight species attributable to the genus *Concavissimisporites* and three species of *Trilobosporites*. A few bisaccate pollen grains, including *Vitreisporites pallidus*, have been recovered, but the gymnospermous pollen spectrum is clearly dominated by the cheirolepidiaceous genus *Classopollis*, its abundance diminishing progressively upwards from units An4 to An2. The great abundance and diversity of verrucate forms, along with the presence of other spores

typical of Lower Cretaceous deposits, such as *Aequitriradites verrucosus*, and the scarcity of specimens referable to *Cicatricosisporites*, render this assemblage most similar to those of the Hastings Group of southern England, and the Bückeberg Formation in north-western Germany. The time of deposition is, therefore, more likely to have been Berriasian–Valanginian rather than Hauterivian–Barremian, as previously stated. The associated small assemblage of megaspores is consistent with this determination. Except for *Trilobosporites* and *Concavissimisporites*, the use of several other genera commonly applied to Mesozoic verrucate spores, such as *Converrucosisporites* and *Impardecispora*, is considered unnecessary. To support this assertion, a Principal Components Analysis has been carried out on 120 verrucate spores from sedimentological units An2–4, taking into account ten morphological variables. The results show that specimens attributable to *Trilobosporites* are well be separated from the main cluster, which corresponds to *Concavissimisporites*, underlining the futility of using more than two genera for the species concerned.

Keywords: verrucate spores; Lygodiaceae; Schizaeaceae; megaspores; Wealden facies; Berriasian; Valanginian; Charentes.

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1. Introduction

Comparatively little is known about the palaeontological content of French Lower Cretaceous continental deposits, mainly because of the scarcity of outcrop. In this connection, the lignitic bone-bed of Angeac in south-west France is remarkable in providing a rare glimpse of the terrestrial palaeoenvironment in this part of the world. The flora and fauna were described by Néraudeau et al. (2012). Since the discovery of the site in 2008, hundreds of ornithomimosaur bones have been found (Allain et al., 2014), along with other vertebrate remains, reminiscent of the fossil record from the Wealden succession of southern England and Wealden-type facies in Spain.

Apart from the deposits of Angeac (Néraudeau et al., 2012), Cadeuil (Platel et al., 1976) and Saint-Agnant (Vullo et al., 2012), no other outcrops of Wealden-type facies have been described from south-western France. They have, however, been encountered in boreholes at Saint-André de Lidon (Ternet and Berger, 1968), Soubran (Kromm et al., 1970), and Saint-Romain-de-Benet (Deák and Combaz, 1967). The last of these yielded a rich palynological assemblage that was considered by Deák and Combaz (1967) to be Valanginian–Hauterivian in age. A few lowest Cretaceous outcrops, corresponding to “Purbeck facies”, have also been reported from the island of Oléron (Lantz, 1958) and from Cherves-Richemont (Bourgueil et al., 1986; Colin et al., 2004; Benoit et al., 2017) (Fig. 1A).

Until recently, the time of deposition of the Angeac sediments was considered to be Hauterivian–Barremian. Although it was noted in Néraudeau et al. (2012, p. 5) that verrucate spores tend to be especially common in deposits of Berriasian–Valanginian age, this younger determination was based on the basis of the recovery of a dinoflagellate cyst (dinocyst) identified as *Odontochitina imparilis* (Duxbury) Jain et Khowaja-Ateequzzaman. However, this age was questioned by Benoit et al. (2017), who dated the deposits as Berriasian owing to the recovery of the charophyte *Clavator grovesii* var. *grovesii* (Harris) Martin-Closas. The

aim of our paper is, therefore, to re-assess the composition of the continental palynological assemblage recovered from Angeac in the light of this recent development. We also discuss the taxonomy of Early Cretaceous verrucate spores.

2. Geological setting

The Angeac site (45° 37' 59.08" N–0° 5' 7.27" W) is situated 700 m north of the village of Angeac-Charente, between Angoulême and Cognac (Fig. 1A). The lignitic beds of "Wealden-facies" underlie Pleistocene alluvium laid down by the Charente River. Seven sedimentological units, An1–An7, were described by Néraudeau et al. (2012) from the top to the base respectively. An1 is composed of 0.10–0.20 m of fine white sand, with abundant fish micro-remains: it was mainly exposed during the first excavation campaigns of 2010 and 2011. An2 comprises 0.20–0.40 m of yellow and grey calcareous and marl deposits, with numerous dinosaur bones, other vertebrate remains, ostracods, charophytes, and pieces of wood (Fig. 1B). The stratification of this bed is difficult to determine because it has been affected by the trampling of dinosaurs (dinoturbation). An3 is a calcareous conglomerate 0.20–40 m thick, with abundant vertebrate remains, ostracods, charophytes, insect coprolites, pieces of wood and other plant debris (Colin et al., 2011; Néraudeau et al., 2012; Benoit et al., 2017). An4 is about 0.5–1.20 m thick. It is composed of blue-grey lignitic clay, oxidized at the top, and has yielded numerous plant and well-preserved vertebrate remains. The base of An5 is not visible. It is more than 0.7 m thick and composed of green clay that is devoid of macrofossils, and includes sub-angular limestone blocks that are likely to have been reworked into this deposit (Néraudeau et al., 2012). An6 and An7 consist of grey limestone and red clay respectively, but they were only seen in 2010, after the initial trench was extended laterally. They did not yield any fossils.

3. Material and methods

3.1. Material and laboratory processing methods

Six samples were processed by E. Masure in order to provide the palynological results presented in Néraudeau et al. (2012). Duplicates of these preparations (LEM1–LEM6) were sent to one of us (DJB) in 2011 and these have now been (re)-examined for this paper. LEM1 comes from the An2 unit (Fig. 1B). LEM2 and LEM3 are from the An3 unit. LEM2 corresponds to the organic fraction in which the size of the particles ranges between 10 and 63 µm, whereas LEM3 includes particles ranging in size from 10 and 100 µm. LEM4 comes from the boundary between units An3 and An4. LEM5 is from the boundary between An4 and An5, and LEM6 comes from within the An5 unit. There was no palynological preparation from the An4 unit. However, a sample from this unit was processed in 2010 by DJB at Aberystwyth University, Wales (preparation QPR 3669: QPR is an Aberystwyth University, palynological preparation identifier), using a standard procedure involving immersion of the sample in 10% HCl followed by digestion in 58–62% HF and brief oxidation of the organic residue in fuming HNO_3, washing after each stage until the residue was neutral (for further information, see Batten, 1999).

Four samples were also processed in Aberystwyth for their mesofossil content: preparations MFP422 from the boundary between An3 and An4, and MFP415, MFP423 and MFP512 from unit An4. All yielded very small assemblages of megaspores. Their extraction involved initial soaking of 100 g of rock in warm water on a hot plate followed by immersion of the sample in a solution of $Na_4P_2O_7$ in order to disaggregate it as much as possible before sieving over a 70 µm mesh to reduce its bulk prior to standard palynological processing using HCl and HF. The megaspores were picked out of the aqueous residues under a

stereomicroscope and housed dry in micropalaeontological slides. Some of the specimens recovered were mounted on scanning electron microscope (SEM) stubs to which carbon tabs had been fixed, coated with platinum–palladium, and examined under a Hitachi S47-100 SEM in the Institute of Biological, Environmental and Rural Sciences (IBERS), Aberystwyth University.

3.2. Specimen counts

For palynological preparations LEM1–LEM4, and QPR 3669, 250 specimens were counted from the slides under a light microscope. LEM5 yielded just 94 specimens, and only a few examples of *Classopollis* were recovered from LEM6.

3.3. Analysis of verrucate spores

Owing to their morphological resemblance to the products of the extant fern *Lygodium*, Cretaceous verrucate spores are considered to belong to the Schizaeales (Bolchovitina, 1961; Ivanova in Samoilovitch and Mtchedlishvili, 1961; Fensome, 1987: see Discussion, Section 5). From the 1950s to the late 1980s, tens of species of eight genera (*Concavissimisporites*, *Converrucosisporites*, *Impardecispora*, *Maculatisporites*, *Rubinella*, *Trilobosporites*, *Tuberositriletes* and *Varirugosisporites*) were erected to accommodate upper Mesozoic verrucate spores, principally on the basis of the outline of their amb, and the size and arrangement of the verrucae on a specimen. This led to considerable overlap between generic and specific diagnoses (Potonié and Kremp, 1954; Delcourt and Sprumont, 1955; Döring, 1964; Venkatachala et al., 1969; Dörhöfer, 1977), as previously underlined and discussed by Batten (1986).

The history of classification of these spores is well summarized by Fensome (1987, pp. 19, 20), who broadened the diagnosis of *Concavissimisporites*, and considered

Tuberositriletes and *Impardecispora* to be junior synonyms. *Tuberositriletes* was erected by Döring (1964) to accommodate Mesozoic forms similar to *Converrucosisporites* Potonié et Kremp, 1954, because he considered the Carboniferous holotype of the type species of the latter to be an atypical developmental stage. Venkatachala et al. (1969) designated *Impardecispora apiverrucata* (Couper, 1958) as the type of *Impardecispora*. This species had previously been accommodated in *Trilobosporites*, a genus that is distinguishable from *Concavissimisporites* by the fact that it possesses one or several valvae at each apex, and/or displays a more or less complete network of muri in the apical region (Fensome, 1987). Srivastava (1977) considered *Maculatisporites* Döring, 1964 to be a junior synonym of *Concavissimisporites*, but Fensome (1987, p. 19) noted that the morphological features of the type species, *M. undulatus* Döring, 1964 do not clearly demonstrate this. The genera *Rubinella* and *Varirugosisporites* were erected by Maljavkina (1949, emended by Potonié, 1960) and Döring (1965) respectively to accommodate Jurassic verrucate forms, but have rarely been used by other authors. The diagnoses of both are very broad and can easily be accommodated within Fensome's (1987) emended diagnosis of *Concavissimisporites*.

A few years later, Waksmundzka (1992) adopted an even more reductive approach and placed *Converrucosisporites*, *Concavissimisporites*, *Converrucitriletes*, *Gemmatriletes*, *Tuberositriletes*, *Maculatisporites*, *Rubinella* and *Varirugosisporites* in synonymy with *Verrucosisporites*. She considered the basis for separation of these genera was insufficient, this being mainly the general outline of the spores. However, *Verrucosisporites* was established by Ibrahim (1933), and emended later by Potonié and Kremp (1954) and Krutzsch (1959), among others, to accommodate Palaeozoic spores covered with warts or small verrucae, which more closely resemble those produced by the Osmundaceae than the Lygodiaceae. Also, placing in synonymy too many taxa can defeat the purpose of achieving a sensible, stratigraphically and biologically relevant taxonomy. Indeed, Waksmundzka (1992,

p. 47) noted that the spores belonging to her emended version of *Verrucosisporites* are imprecisely related to the Pteridophyta. Hence, we do not accept her solution to the problem of too many genera for verrucate miospores. We prefer to base our identifications on Fensome's major revision (1987) which, despite his synthesis and practical approach, has never been discussed, most of the genera noted above still being encountered in the literature (e.g., Burden and Hills, 1989; Song et al., 2000; Dejax et al., 2007). This not only renders comparisons between assemblages challenging, but also diminishes the stratigraphic significance of the species, because too many names are available for the same morphotype and closely similar forms.

As a result, it was decided to carry out a Principal Components Analysis (PCA) of the verrucate spores in the Angeac palynomorph assemblages, one of the purposes being to determine whether *Concavissimisporites* can truly be regarded as encompassing a morphological group that is well separated from *Trilobosporites* (see Section 4.2.). Indeed, since numerous verrucate spores were recovered from the samples corresponding to sedimentological units An2–4, we decided to identify them *a priori* following Fensome's emended diagnoses as species of either *Concavissimisporites* or *Trilobosporites*. The PCA was then carried out using 120 specimens from the three units (50, 20, and 50 for An2, An3 and An4, respectively). The purposes of this statistical analysis were to see whether it is possible to (1) obtain several morphological groups that would cluster according to the diagnoses of already established species, (2) determine those groups that can be divided into two or more genera, and (3) ascertain whether there are any significant morphological differences between the specimens recovered from the different lithological units.

Ten variables were taken into account (Fig. 2):

S: size of specimen (= maximum diameter).

SA: smallest value of the reflex, acute or obtuse angle formed by the two tangents of the starting and arrival points of the arc or curve formed by the outline of the interradial region of a spore.

LA: largest value of the reflex, acute or obtuse angle formed by the two tangents of the starting and arrival points of the arc or curve formed by the outline of the interradial region of a spore.

MiD/MaD: ratio between the minimum and maximum distances from the centre to the edge of the spore (excluding the verrucae).

mDV: mean diameter of verrucae on one spore; 32 verrucae were counted on each specimen, when possible. Most of the means have been calculated based on approximately 20 values.

mHV: mean height of verrucae on one spore.

STDV: standard deviation of the diameter of verrucae on one spore.

STHV: standard deviation of the height of verrucae on one spore.

ET: exine thickness.

PC: per cent cover of the verrucae on the proximal face of a spore. 0.15: 0–30%; 0.45: 31–60%; 0.75: 61–94%; 0.95: 95–100%.

All of the values have been divided by the size of the specimen, and scaled. They were measured on clear images of the specimens under a light microscope. The angles were measured using the free java application *OnScreenProtractor*. The various lengths and diameters were measured using the software *Inkscape*. The PCA was carried out using the software *Past*.

3.4. Repository

All of the palynological preparations and the megaspores illustrated are housed in the Geological Institute of the University of Rennes 1, under collection numbers IGR-PAL-5735–

IGR-PAL-5753 for the palynological slides, and IGR-PAL-5780–IGR-PAL-5784 for the megaspores illustrated.

4. Results

4.1. Palynological assemblages

Altogether 34 taxa (excluding those placed in comparison apart from *Concavissimisporites* sp. cf. *C. crassatus*) have been identified at genus or species level in the seven samples examined (Fig. 3). The most common of these are the cheirolepidiaceous pollen grain *Classopollis* (Fig. 4C, D), verrucate spores such as *Concavissimisporites montuosus* (Döring) Fensome (Fig. 5J, K, M), *Concavissimisporites apiverrucatus* (Couper) Döring (Fig. 5A, B), *Concavissimisporites exquisitus* (Singh) Fensome (Fig. 5C, D) and *Trilobosporites canadensis* Pocock (Fig. 6H), the papillate spore *Pilosisporites trichopapillosus* (Thiergart) Delcourt et Sprumont (Fig. 4P), the hilate spore *Aequitriradites verrucosus* (Cookson et Dettmann) Cookson et Dettmann (Fig. 4G), and various smooth walled spores belonging to the genera *Cyathidites*, *Deltoidospora*, and *Gleicheniidites* (Fig. 4H, J). Freshwater algae such as *Ovoidites spriggi* (Cookson et Dettmann) Zippi (Fig. 4N) are relatively common, but no more dinoflagellate cysts were encountered during the re-examination.

An2 yielded an assemblage of 16 species (Fig. 3), numerically and taxonomically dominated by verrucate spores (Fig. 7). It is the only assemblage in which there are no *Classopollis* pollen, the gymnosperm component being represented by only two inaperturate pollen grains referable to *Araucariacites australis* Cookson. Eighteen species were recovered from the An3 unit. Verrucate spores are less diverse than in the An2 unit with eight species, but the gymnosperms are better represented, with numerous specimens referable to

Classopollis torosus (Reissinger) Couper, and bisaccates such as *Abietineaepollenites* sp. (Fig. 4A). This is the only assemblage in which a specimen of *Cicatricosisporites hallei* Delcourt et Sprumont was found (Fig. 4M). The sample taken from the boundary between An3 and An4 yielded 16 species, five of which are exclusive to this sample: *Callialasporites dampieri* (Balme) Dev (Fig. 4B), *Densoisporites microrugulatus* Brenner (Fig. 4K), cf. *Foraminisporis wonthaggiensis* (Cookson et Dettmann) Dettmann (Fig. 4L), *Microreticulatisporites* sp. cf. *M. diatretus* Norris (Fig. 4I), and *Podocarpidites ellipticus* Cookson (Fig. 4F). The assemblage from the lignitic clays of An4 is the most diverse, having yielded 21 species, three of which were recorded only from this level: *Retitriletes* sp. (Fig. 4O), *Cerebropollenites mesozoicus* Couper, and *Vitreisporites pallidus* (Reissinger) Nilsson (Fig. 4E). This sample yielded proportionally the greatest abundance of *Classopollis* (Fig. 7), but also, and in common with An2, the most diverse verrucate spore assemblage (nine species). The An4/An5 sample yielded a moderately diverse, albeit small assemblage of 15 species, including six verrucate taxa. Overall, the relative abundance of *Classopollis* tends to decrease upwards in the succession from An4/An5 to An2, whereas the abundance of the verrucate and smooth walled spores increases greatly in this direction.

Also, significant in this context is the fact that specimens identified as *Trilobosporites* are more abundant in the palynomorph assemblage recovered from An2 than in the older deposits, and that overall, verrucate spores in the An2 assemblage are generally larger and more sparsely sculptured than those recovered from the other units (see PCA plots, Figs 8, 9).

4.2. Megaspores

The four samples processed for their mesofossil content yielded only a few megaspores and fragments thereof, most of which are referable to the genus *Erlansonisporites* (Figs. 10, 11A, B), and faecal pellets, probably attributable to the activities of termites (Colin et al.,

2011). The sample from the boundary between An3 and An4 (preparation MFP422) also proved to contain a few specimens of a form tentatively recorded here as *Minerisporites* sp. (Fig. 11C–F). Apart from a couple specimens that are currently unidentifiable without recourse to examination under an SEM, all other megaspore remains are too damaged or fragmentary to be positively identified: among these are possible representatives of *Paxillitriletes*. Associated with the megaspores in MFP422 are isolated, comparatively large specimens of the freshwater algae *Schizosporis reticulatus* Cookson et Dettmann emend Pierce and *Ovoidites spriggii* (Cookson et Dettmann) Zippi.

Most of the specimens of *Erlansonisporites* (Figs. 10E, F, 11A, B) are closely similar to *Erlansonisporites* sp. *sensu* Batten, 1975, pl. 13, fig. 6, a selaginellalean megaspore from the upper Berriasian–Valanginian Ashdown Formation in Sussex, south-east England (e.g., Batten, 2011): this is consistent with the suggested revised age determination of the Angeac deposits herein. Numerous microspores, all exhibiting the same morphology, are lodged within the muri of its reticulate sculpture, especially on the proximal surface close to the triradiate flange. In the dispersed state, these are probably attributable to the small spore genus *Patellasporites*, or perhaps *Uvaesporites*.

The specimens of *Minerisporites* sp. are atypical for this genus in that, although zonate, they have a virtually smooth surface and a triradiate flange that is of uneven elevation, indeed it can be partly spinose (Fig. 11C). The outer edge of the zona is also uneven to weakly spinose, features that might equally suggest a representative of *Henrisporites*, albeit again atypical. More specimens are required before this form can be satisfactorily identified.

4.3. Systematic palaeontology of the verrucate spores

The PCA2 plot (Fig. 9) supports Fensome's (1987) taxonomic approach to the identification of verrucate spores, the specimens from Angeac only being attributable to two

genera, *Concavissimisporites* and *Trilobosporites*. They are morphologically well separated, principally on the account of their size, the relative size of their verrucae, and the variation in the dimensions of verrucae on a specimen. Three species of *Trilobosporites*, and eight species of *Concavissimisporites* have been identified, along with several intermediate forms. Except for *Concavissimisporites apiverrucatus*, specimens assigned to a particular species are clustered together, although the boundaries between the clusters are not always clearly defined. It was thought that the semi-quantitative variable corresponding to the per cent cover of verrucae (PC) might be biasing the results of the PCA in assuming too much importance compared to the other variables. Thus, another PCA was run without the per cent cover variable, but the results were very similar, indicating that this did not significantly affect the plot.

Genus *Concavissimisporites* Delcourt et Sprumont, 1955, emend. Fensome, 1987.

Type species: *Concavissimisporites verrucosus* Delcourt et Sprumont, 1955 emend. Delcourt et al., 1963.

Concavissimisporites apiverrucatus (Couper, 1958) Döring, 1965 (Fig. 5A, B)

Material. Angeac units An2, An3/4, An4, An4/5: 11 specimens, 57 (72) 105 µm in diameter.

Remarks. Concavissimisporites apiverrucatus is differentiated from the other species of this genus in that the sculpture of the apices is slightly to distinctly coarser than over the poles and in interradial regions. In the case of the Angeac specimens, the polar and interradial regions are almost smooth (Fig. 5B), granulate (Fig. 5A), or sculptured with verrucae. Specimens attributed to this species are the only ones that do not form a united cluster on PCA2 (Fig. 9),

principally because the main diagnostic characters mentioned above have not been considered as a variable, these being very difficult to calculate.

Occurrence. This species occurs widely in rocks ranging in age from latest Jurassic to Albian (e.g., Fensome, 1987; Burden and Hills, 1989). In France, it has been recorded, as *Trilobosporites apiverrucatus* Couper, from "Wealden" (Delcourt and Sprumont, 1959), lower Valanginian (Vakhrameev and Kotova, 1980), upper Barremian–lower Aptian (Herngreen, 1971) and upper Albian (Bardet et al., 1991) deposits.

Concavissimisporites sp. cf. *C. crassatus* (Delcourt et Sprumont, 1955) Delcourt et al., 1963 (Fig. 5L, N)

Material. Angeac unit An2: three specimens 61 (63) 67 µm in diameter.

Remarks. Specimens Q35.4 and B28.4 (Fig. 5L, N) fit the description given by Delcourt et al. (1963, p. 285), bearing in mind the changes made by Fensome to the generic diagnosis (1987, p. 19). No formal size range is given by Delcourt et al., but their illustrated specimen is 78 µm in diameter. Delcourt and Sprumont (1955, p. 26) stated that the "radius" of their form *crassatus* is 40–55 µm. As a result, we only compare our specimens to this species because they are smaller.

On the PCA2 (Fig. 9), the squares pertaining to *C.* sp. cf. *crassatus* are situated at the edge of the cluster that corresponds to *C. montuosus*. It could be argued that these specimens are also identifiable as *C.* sp. cf. *C. montuosus*, the limiting character being the small size of the verrucae.

Occurrence. Concavissimisporites crassatus was originally described from Wealden-type strata in Belgium (Delcourt and Sprumont, 1955; Delcourt et al., 1963). It has not been encountered previously in France, but has been found in Albian strata of the Bay of Biscay

(Batten, 1979), Berriasian–mid-Valanginian strata in the Netherlands (Burger, 1966), upper Berriasian, and upper Barremian–lower Aptian rocks in Germany (Dörhöfer, 1977; Lister and Batten, 1995), and within Cenomanian deposits of Spain (Solé de Porta, 1978). It was also recorded by Fensome (1987) from Upper Jurassic to lower Valanginian strata in western Canada.

Concavissimisporites exquisitus (Singh, 1971) Fensome, 1987 (Fig. 5C, D)

Material. Angeac units An2, An3, An3/4, An4, An4/5: 19 specimens, 47 (59) 75 µm in diameter.

Remarks. This species is defined by its triangular to convex outline, coupled with bulbous verrucae 6–10 µm wide. In his original diagnosis, Singh (1971, p. 116) stated that the verrucae are spaced 1–4 µm apart. The verrucae on the specimens from Angeac are more closely spaced overall, being separated by no more than 1 µm. The size-range given by Singh is 68 (71) 84 µm, but this is based on only four specimens, and the only specimen of this species recovered by Fensome is 59 µm in diameter (1987, pl. 4, fig. 11). Some relatively small, rounded specimens, such as R40.2 (Fig. 5E), are referred to *Concavissimisporites* sp. cf. *C. exquisitus* because they show proportionally smaller verrucae. They are more similar to *Verrucosisporites major* (Couper) Burden et Hills, a form that occurs widely in Jurassic and Cretaceous strata.

The cluster corresponding to this species on the PCA2 plot is very close to that representing *Concavissimisporites ferniensis* (Fig. 9), which is, however, distinguished from *C. exquisitus* in having significantly lower verrucae separated by narrow canals that form a more or less distinct negative reticulum.

Occurrence. This species was originally recovered from Albian strata in Alberta, Canada (Singh, 1971), but Fensome (1987) found it in upper Jurassic deposits. It has not been encountered previously in France, but Mohr (1989) mentioned its presence in upper Tithonian–lower Berriasian strata in Portugal.

Concavissimisporites ferniensis (Pocock, 1970) Fensome, 1987 (Fig. 5F–H)

Material. Angeac units An2, An3, An3/4, An4: seven specimens 45 (56) 78 µm in diameter.

Remarks. For differences between *Concavissimisporites ferniensis* and *C. exquisitus*, see remarks above under the latter species. In common with *C. exquisitus*, the specimens assigned to *C. ferniensis* are very similar to *Verrucosisporites major*, which however differs in usually being smaller and in lacking a negative reticulum (see Couper, 1958).

Occurrence. This species has only been recovered from Jurassic sedimentary rocks in western Canada (Fensome, 1987), but very similar forms, identified as *Leptolepidites major* Couper, have been found in various French Jurassic, Albian and Cenomanian strata (Fauconnier, 1979; Fechner and Dargel, 1989; Bignot et al., 1994).

Concavissimisporites montuosus (Döring, 1964) Fensome, 1987 (Fig. 5J, K, M)

Material. Angeac units An2, An3, An3/4, An4, An4/5: 26 specimens 52 (72) 105 µm in diameter.

Remarks. This species is characterized by being sculptured with typically well-spaced verrucae 2–5 µm in diameter. It is the most common verrucate spore in the Angeac succession. A few specimens have been referred to *Concavissimisporites* sp. cf. *C. montuosus* (e.g., N26.1, not illustrated), because they have more closely spaced and smaller verrucae.

Occurrence. The stratigraphic range of *Concavissimisporites montuosus* extends from upper Oxfordian to Albian. It is a distinctive element in many Volgian–Valanginian palynofloras (Fensome, 1987). It has not been found in France previously, but has been recovered, as *Converrucosisporites montuosus* Döring, from lowest Cretaceous strata in north-western Germany (Dörhöfer and Norris, 1977). According to these authors, an abundance of this form is characteristic of their upper Berriasian palynofloral suite "Hils 1".

Concavissimisporites robustus Dörhöfer, 1977 (Fig. 5I)

Material. Angeac units An2, An3: two specimens 59 and 66 µm in diameter.

Remarks. *Concavissimisporites robustus* differs from the other species encountered in having a more or less uniformly thick exine coupled with poorly delineated verrucae that are either sparsely or densely distributed. The two specimens recovered from Angeac are weakly sculptured. The PCA2 plot shows that they cluster closest to the specimens identified as *C. uralensis*, mainly because of the scarcity of the verrucae on the proximal face.

Occurrence. This species was originally described from the upper Berriasian palynofloral suites "Hils 1" and "Hils 2" in north-western Germany (Dörhöfer, 1977). It has also been recorded from uppermost Jurassic strata in western Canada (Fensome, 1987) and middle Berriasian deposits in eastern Maryland, USA (Doyle, 1983).

Concavissimisporites uralensis (Bolchovitina, 1961) Fensome, 1987 (Fig. 6D)

Material. Angeac units An2, An4: three specimens 56 (68) 90 µm in diameter.

Remarks. This species can appear very similar to the specimens identified here as *Concavissimisporites apiverrucatus*: they differ in being more sparsely sculptured. They also

differ from specimens of *C. robustus* in having a thinner exine. It could be argued that they are intermediate between *C. apiverrucatus* and *C. robustus*. However, the PCA clustered all three specimens together, quite far away from the other clusters, which is why we decided to regard them as belonging to a distinct species (see Section 6.2 for the biological relevance of this decision).

Occurrence. *Concavissimisporites uralensis* was originally described from Barremian–Aptian strata in western Kazakhstan (Bolchovitina, 1961). It has also been recorded from Ryazanian (lowest Berriasian) strata in western Canada (Fensome, 1987).

Concavissimisporites verrucosus Delcourt et Sprumont, 1955 emend. Delcourt et al., 1963 (Fig. 6A, B)

Material. Angeac units An3, An4, An4/5: six specimens 73 (81) 100 µm in diameter.

Remarks. This species differs from the other verrucate spores from Angeac by its large size, and in having relatively small, closely spaced verrucae. The specimen D20.4 (Fig. 6C) is considered to be an intermediate form between *C. verrucosus* and *C. montuosus*, because it is sculptured with relatively large, closely spaced verrucae.

Occurrence. The stratigraphic range of *C. verrucosus* extends from Middle Jurassic to Lower Cretaceous. In western Europe, it occurs principally within lowest Cretaceous and "Wealden"-type strata (Burger, 1966; Bolchovitina, 1971; Dörhöfer and Norris, 1977).

Genus *Trilobosporites* Pant, 1954 ex Potonié, 1956 emend. Fensome, 1987

Type species: *Trilobosporites hannonicus* (Delcourt et Sprumont, 1955) Potonié, 1956

Trilobosporites aequiverrucosus Dörhöfer, 1977 (Fig. 6I)

Material. Angeac unit An4: one specimen, 100 µm in diameter.

Remarks. This species differs from *Trilobosporites canadensis* in having proportionally smaller unfused, closely spaced verrucae in polar and interradial regions. As stated by Dörhöfer (1977, pp. 53, 54), this species is considered to include many specimens previously attributed to *Trilobosporites bernissartensis* (Delcout et Sprumont) Potonié, for which the type and size of the sculptural elements were not specified. The re-illustrations of the holotype and paratypes in Delcourt et al. (1963, pl. 43, figs. 11–14) are considered inadequate, because several morphotypes are displayed. As a result, Dörhöfer considered that a precise interpretation of *T. bernissartensis* is not possible.

Occurrence. The species was originally described from upper Berriasian–lower Valanginian beds in western Germany (Dörhöfer, 1977). As *Trilobosporites bernissartensis*, it has been found in Wealden-type strata in Belgium (Delcourt and Sprumont, 1955; Delcourt et al., 1963), and in Purbeck and Wealden beds in southern England and stratigraphically equivalent deposits in western France (Couper, 1958; Lantz, 1958; Deák and Combaz, 1967). It has also been reported from lowest Aptian strata in south-eastern France (de Reneville and Raynaud, 1981), and within upper Barremian–lower Aptian strata in northern France (Herngreen, 1971). However, the specimen illustrated by Herngreen (1971, pl. 3, fig. 1) is in fact attributable to *Trilobosporites hannonicus* (Delcourt et Sprumont) Potonié, so we do not accept this record of occurrence.

Trilobosporites aornatus Döring, 1965 (Fig. 6E, F)

Material. Angeac units An2, An3, An4: three specimens 68 (78) 96 µm in diameter.

Remarks. The morphology of the specimens recorded as *Trilobosporites aornatus* have a maculate sculpture and a large verruca or rounded valva in equatorial radial regions. K28.3 (Fig. 6G) is referred to *Trilobosporites* sp. cf. *T. aornatus*, because of the presence of a few verrucae close to each of the angles, in common with the specimen illustrated by Norris as *Trilobosporites obsitus* Norris (1969, pl. 106, fig. 7) (see Section 5.2. for the biological relevance of this species).

Occurrence. Döring (1965) described this species from Upper Jurassic–lowermost Cretaceous strata in eastern Germany. In southern England, it is typical of the upper Berriasian–lower Valanginian palynofloral suite C of Norris (1969), and as discussed by Dörhöfer and Norris (1977). In North America, it ranges into the lower Barremian (Burden and Hills, 1989).

Trilobosporites canadensis Pocock, 1962 (Fig. 6H)

Material. Angeac units An2, An3, An3/4, An4, An4/5: 11 specimens 69 (88) 105 µm in diameter.

Remarks. *Trilobosporites canadensis* is characterized by its coarse interradial and polar verrucae, which sometimes merge to form elongate elements, along with one or two large, pronounced, strongly projecting verrucae or valvae in equatorial radial regions. This is the most common form of *Trilobosporites* at Angeac, especially in the An2 unit.

Occurrence. This species was originally described from “Neocomian” deposits in western Canada (Pocock, 1962). In Western Europe, it has been reported from upper Berriasian–lower Valanginian beds in western Germany (Dörhöfer, 1977), probable Berriasian Purbeck beds in southern England (as *T*. cf. *canadensis*; Hunt, 1985), Tithonian–Berriasian deposits in Portugal (Mohr, 1989) and within upper Barremian–lower Aptian strata in northern France (Herngreen, 1971). However, the morphology of the specimens illustrated in Herngreen’s

paper (pl. 3, figs. 2–4) is closer to that of *Concavissimisporites montuosus* than to *T. canadensis*.

5. Discussion

5.1. Age determination and comparisons

We discuss the previous identification in Néraudeau et al. (2012) of the dinoflagellate cyst *Odontochitina imparilis* (Duxbury) Jain et Khowaja-Ateequzzaman in the Angeac assemblage. In his description of *Muderongia imparilis*, Duxbury (1980, p. 128) indicated the presence of three well-developed horns as a diagnostic feature, with the lateral horn being greatly reduced. A lateral horn seems to be present on the Angeac specimen, but it is folded behind the periblast. There are two antapical horns, one shorter than the other. The longer of the two is very corroded. A vestigial apical horn is present. The original description also states that the endoblast and periblast are joined together in the epicystal region, which does not seem to be the case of the Angeac specimen, the endoblast being proportionally much smaller than the periblast.

The species has usually been found within Hauterivian–Barremian deposits (Duxbury, 1980; Jain and Khowaja-Ateequzzaman, 1984; Leereveld, 1997), hence the previous attribution of a Hauterivian–Barremian age to the Angeac deposits. However, the species has also been recorded from upper Valanginian strata (Burger, 1996). Although the poor preservation of the Angeac specimen renders the identification questionable, the short range of the species may well be related to the general scarcity of this form and linked to specific environmental conditions (Masure, pers. comm. 2017), so a find of *O. imparilis* in older deposits is not impossible.

The Angeac specimen is also similar to *Muderongia simplex* Alberti, which has one apical, two lateral, and two antapical horns. The holotype of this species is 151 µm long, which is almost the same as the Angeac specimen at 152 µm. However, they differ in that the latter possesses a proportionally small endoblast, and does not display a second lateral horn, although it is possible that has been destroyed or is obscured by folding. The stratigraphic range of *Muderongia simplex* extends from upper Tithonian to upper Valanginian (Riding et al., 2000).

Dating Lower Cretaceous deposits using miospores can be challenging, the forms encountered often being long ranging. For instance, *Aequitriradites verrucosus* and *Pilosisporites trichopapillosus* are present through all of the Lower Cretaceous in western Europe. In France, *A. verrucosus* has only been reported recently within Cenomanian deposits (Fleury et al., 2017). Batten (1979) recorded it from Aptian–Albian strata in the Bay of Biscay. It occurs rarely elsewhere in Europe but has nonetheless been documented from Aptian and Wealden deposits in England (Ruffell and Batten, 1994 and Batten unpublished, respectively) and in Wealden-type facies in Germany (Döring, 1964).

Pilosisporites trichopapillosus ranges from uppermost Jurassic (Couper and Hughes, 1963) to Upper Cretaceous (Robaszynski et al., 1985), but is more frequently recovered from Lower Cretaceous deposits (Bolchovitina, 1971; Dörhöfer, 1977; Batten, 1979; Doubinger and Mas, 1981; Batten and Li, 1987). In France, it has only been documented from Tithonian strata (Couper and Hughes, 1963).

Nevertheless, dating can be more precise if the composition of entire assemblages is taken into account. A few attempts at stratigraphic correlations using Lower Cretaceous miospore assemblages were made during the late 1960s and early 1970s. A method introduced by Hughes and Moody-Stuart (1969) consisted of using several types of *Cicatricosisporites* to correlate between different beds in a Wealden borehole and an outcrop

549 in south-east England. Their abandonment of Linnaean nomenclature in favour of biorecords
550 (Hughes and Moody-Stuart, 1969; Hughes, 1970) meant that their method did not gain
551 widespread support among palynologists (Batten, 1986). Regardless, we could not apply a
552 similar approach to the Angeac assemblages using species of *Cicatricosisporites* because only
553 a few specimens of this taxon were recovered.

554 Another method involved the use of palynological assemblage-types for correlating
555 Wealden deposits in southern England (Batten, 1973). Seventeen assemblages were described,
556 taking into account preservation state, diversity of miospores, average size of trilete spores,
557 abundance of brown wood, and the abundance of certain taxa. The total Angeac assemblage
558 (i.e. the overall composition of the assemblages recovered from An2–5) is very similar to
559 Batten's Assemblage Type 15 (AT 15). This was characterized by the common presence of
560 *Concavissimisporites*, coupled with a "Trilete spore content dominated by average-sized or
561 large forms; miospore diversity average or large; general state of preservation of miospores
562 good or fair; brown wood and cuticle P, C or F [present, common, or frequent]; *Pilosisporites*
563 P or C [present or common], *Cicatricosisporites* C or V [common or very
564 common]…..*Trilobosporites* occurs in more than 70% of the assemblages referable to this
565 AT" (Batten, 1973, pp. 13, 14). The only difference from this description is the scarcity of
566 *Cicatricosisporites*. Following the same study, and using current stratigraphic terminology
567 (e.g., Batten, 2011), this assemblage-type has mostly been recovered from the Ashdown
568 Formation, including the Fairlight Clays facies, and the Grinstead Clay Formation, all of
569 which are part of the Hastings Group, which was deposited between the mid Berriasian and
570 the late Valanginian.

571 The Angeac assemblage overall is also very similar to those recovered from the
572 Bückeberg Formation, especially the upper Berriasian palynofloral suites "Hils 1" and "Hils
573 2", which are characterized by abundant *Concavissimisporites montuosus*, large

574 *Trilobosporites*, and the relative scarcity of *Cicatricosisporites* (Dörhöfer, 1977; Dörhöfer and
575 Norris, 1977). In France, Berriasian palynological assemblages have been recovered from
576 Jura (eastern France) and potentially Oléron island (Fig. 1). The Angeac assemblage is
577 somewhat similar to that recovered by Médus and Mojon (1991) from upper Berriasian strata
578 of southern Jura in that the latter is characterized by an abundance of *Densoisporites*
579 *microrugulatus* and *Trilobosporites*. It was compared to palynofloral suite "Hils 4" (Médus
580 and Mojon, 1991, p. 57), but only a few illustrations were provided to support the
581 identifications, and *D. microrugulatus* is not abundant in the Angeac assemblage. The
582 uppermost Berriasian assemblage from Jura recovered earlier by Taugourdeau-Lantz and
583 Donze (1971) is less similar, with few verrucate spores and several dinoflagellate cyst species
584 in association. The palynoflora recovered from the "Purbeck beds" of Oléron island (Lantz,
585 1958) includes similar forms of *Trilobosporites*, but the types of *Concavissimisporites* are less
586 diverse, and the specimens illustrated seem comparatively small.

587 The Angeac assemblage is, however, less clearly correlated with younger palynofloras,
588 such as that recovered from the Wealden-facies, dinosaur-bearing pit of Bernissart (Belgium,
589 Dejax et al., 2007), considered to be Hauterivian in age. The samples from this pit yielded
590 specimens of *Trilobosporites* that are similar to the species *T. hannonicus* (Delcourt et
591 Sprumont) Potonié, which has not been recorded from Angeac, more species of
592 *Cicatricosisporites*, and angiospermid pollen grains. Correlations with the assemblage
593 recovered from Saint-Romain-de-Benet, regarded as Valanginian–Hauterivian in age, are
594 quite difficult to make because of a lack of precision in the description of the assemblage as
595 indicated by such statements as …. "on n'observe pratiquement pas de pollens
596 d'Angiospermes" in Deák and Combaz (1967, p. 72), meaning that they "almost did not
597 observe any angiosperm pollen grains". Their stratigraphic range chart (p. 71) is rather
598 inaccurate because most of the species they note as restricted to the Valanginian–Hauterivian

have, in fact, wider ranges. In any case, they do not seem to have encountered many verrucate spores, and their species of *Trilobosporites* are quite different from those recovered from Angeac.

Although most of the palynomorphs identified herein indicate a stratigraphic distribution that is not confined to the lowest Cretaceous, previous observations in Néraudeau et al. (2012, p. 5) and our new data suggest that the Angeac assemblage is more likely to have been deposited during the Berriasian–early Valanginian rather than in the Hauterivian–Barremian, as previously stated.

5.2. Biological relevance of the verrucate spores

The family Schizaeaceae originally included five extant genera: *Schizaea* Sm., *Actinostachys* Wall., *Mohria* Sw., *Anemia* Sw., and *Lygodium* Sw., which are widely distributed in predominantly tropical or southern warm-temperate parts of the world (Tryon and Lugardon, 1991). However, Smith et al. (2006) considered that these genera in fact belong to three families of the order Schizaeales: Schizaeaceae (for *Schizaea* and *Actinostachys*), Anemiaceae (for *Anemia*, including *Mohria*), and Lygodiaceae (for *Lygodium*).

Unequivocal members of this order first appeared in the Early or Middle Jurassic, but they did not become widespread until the Early Cretaceous, as indicated by occurrences of their spores in numerous deposits throughout Eurasia (Bolchovitina, 1971; Van Konijnenburg-Van Cittert, 2002). The Schizaeaceae produce monolete, bean-shaped spores, with diverse ornamentation. The Anemiaceae have trilete spores with coarse, compact ridges. These have abundant Lower Cretaceous analogues, such as *Cicatricosisporites*, and specimens found *in situ* within fertile plant organs associated with the ferns *Ruffordia*, *Pelletieria*, and *Schizaeopsis* (e.g., Hughes and Moody Stuart, 1966). *Lygodium* spores are

624 trilete, and can be tuberculate, verrucate or reticulate (Tryon and Lugardon, 1991). Thus,
625 Early Cretaceous verrucate spores have often been compared to the genus *Lygodium* (e.g., in
626 Delcourt and Sprumont, 1955; Bolchovitina, 1961; Ivanova in Samoilovitch and
627 Mtchedlishvili, 1961; Fensome, 1987).

628 Mesozoic spores comparable to *Lygodium* have only been found *in situ* in Jurassic rocks
629 in northern England (Van Konijnenburg-Van Cittert, 1981), but they have a reticulate
630 sculpture. They have been encountered in sorophores from Turonian deposits in New Jersey,
631 USA (Gandolfo et al., 2000), and compared to the extant species *Lygodium palmatum*
632 (Bernh.) Sw. on account of their trilete, psilate spores, among other characters. Dispersed
633 spores are much more abundant. Bolchovitina (1961) produced a comprehensive monograph
634 on fossil and extant spores of the former family Schizaeaceae (now Schizaeales), in which she
635 listed 62 species of extant *Lygodium* (Smith et al., 2006 considered that the Lygodiaceae
636 comprise only about 25 species), remarked on and illustrated 27 of these, and listed,
637 commented, described or re-described, and illustrated 46 species of dispersed fossil spores
638 referable to *Lygodium*.

639 The spores of the extant species are usually described according to their shape,
640 thickness of exine, colour and sculpture. The last of these may vary within a species, such as
641 in *L. flexuosum* (L.) Sw. and *L. japonicum* (Thunb.) Sw., which produce smooth to slightly
642 tuberculate spores. However, when a species also displays a coarser sculpture, several authors
643 (e.g., Couper, 1958; Dettmann and Clifford, 1991) have considered associated smooth spores
644 to be immature forms. Spore polymorphism has been recognized in a few anemiaceous
645 species (Dettmann and Clifford, 1991), but it would seem that in general mature spores of
646 extant species of *Lygodium* can be well separated on the basis of their sculpture (Bolchovitina,
647 1961; Tryon and Lugardon, 1991; see also SEM micrographs of *Lygodium* spores in the
648 Cornell University website).

Hence, most of the morphological clusters of the verrucate spore species displayed by PCA2 (Fig. 9) could well also have biological significance. Specimens assigned to *Concavissimisporites uralensis*, which are defined by their weak sculpture, could in fact be immature forms of other species of *Concavissimisporites*. The same applies to *Trilobosporites aornatus*, which could comprise immature specimens of *T. aequiverrucosus* or *T. canadensis*. Intermediate forms such as specimen K28.3 (Fig. 6G) would support this suggestion. The most abundant verrucate spore in the Angeac palynomorph assemblages, *Concavissimisporites montuosus*, is similar to the spores of the extant species *Lygodium circinatum* (Burm. f.) Sw., in that both display quite well spaced, massive verrucae. Specimens assignable to the genus *Trilobosporites* are somewhat similar to the spores of *Lygodium merrillii* Copel., which display coarse distal muri that appear as a thickening of the exine in apical regions on the proximal face. However, no spores of extant species of *Lygodium* seem to develop valvae, which is all the more reason to maintain *Trilobosporites* as a separate genus for fossil spores with this character. Some species of *Concavissimisporites*, such as *Concavissimisporites exquisitus*, also do not seem to have any modern analogues.

5.3. Palaeoenvironmental implications

The great abundance of verrucate spores in the assemblages suggests the presence of ferns showing a strong affinity with species of the extant genus *Lygodium*, a pantropical climbing schizaealean, concentrated especially in Malaysia and Central America (Kramer in Kramer and Green, 1990). These ferns are typical of warm, humid environments. Their fossil analogues may well have grown along riverbanks or in understories of forests (Van Konijnenburg-Van Cittert, 2002). The composition of the Angeac palynological assemblages is consistent with the previous interpretation of the depositional environment at this site as a

swamp, but the absence of marine dinoflagellate cysts apart from the single specimen identified as *Odontochitina imparilis*, suggests very limited connection to the sea (Néraudeau et al., 2012). Nevertheless, this is attested by the relative abundance in unit An2 of brackish ostracods such as *Fabanella boloniensis* (Schudack and Schudack, 2011) and the presence at different levels (An3–4, An1) of a few benthic foraminifers (*Ammocycloloculina* sp., *Trocholina odukpaniensis*) and echinoid or bryozoan debris (Néraudeau et al., 2012 and unpublished data).

No palaeoenvironmental variation has previously been noted for the period of deposition of the sediments comprising units An5–An2. However, the relative composition of Angeac palynological assemblages changes from An4/5 up to An2, the abundance of verrucate spores clearly increasing at the expense of *Classopollis*, which diminishes greatly (Fig. 7). The verrucate spores recovered from unit An2 appear to be generally larger than the specimens recovered from the older units An3 and An4 (Fig. 8).

From a sedimentological perspective, the succession of green clay (An5), dark clay (An4) and calcareous conglomerate (An3), and then of silty limestone (An2) and fine sand (An1) implies two successive sequences of increasing energy in the depositional environment, which suggests progressive flooding of the swamp by a river nearby, ending with the establishment of a floodplain. This environmental change could explain the increase of the abundance of verrucate spores up-section, ferns being generally more abundant than gymnosperms in a floodplain (Coiffard et al., 2006, 2007).

6. Conclusion

Our taxonomic study of the Angeac palynological assemblages provides a rare insight into French palynofloras of Berriasian–Valanginian age. They have previously only been

documented from deposits in the Jura mountains, the Vocontian Basin, and on Oléron island (Lantz, 1958; Taugourdeau-Lantz and Donze, 1971; Médus and Mojon, 1991; Kujau et al., 2013), but the Angeac assemblages seem more continental not only because of the abundance of verrucate spores but also owing to the scarcity of marine indicators in the preparations.

All of the verrucate spores are attributable to either *Concavissimisporites* or *Trilobosporites*, which in turn are believed to have been produced by ferns showing strong affinities with extant *Lygodium*, a fern genus that typically inhabits warm, humid environments. These ferns could well have grown on the margins of the swamp envisaged by Néraudeau et al. (2012) and been widely dispersed on the developing floodplain.

Despite the important work of Bolchovitina (1961, 1971), in the light of recent research on modern representatives of the Lygodiaceae a taxonomic revision of Lower Cretaceous lygodiaceous spores in the Northern Hemisphere is now needed in which both their biological affinities and stratigraphic distribution are taken into account.

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940

941

942 **Figure captions**

943

944 **Fig. 1. A**. Map showing the geographical and geological location of Angeac, along with other
945 outcrop localities and boreholes in which "Purbeck" and Wealden-type facies are preserved.
946 Soubran is mentioned in the introduction (Section 1), but is located about 50 km south-east of
947 Royan, and is not, therefore, indicated on the map. GPS coordinates of the site: latitude: 45°

37' 59.08" N; longitude: 0° 5' 7.27" W. **B**. Synthetic stratigraphic section of Angeac sedimentological units. The solid circles indicate parts of the section from which the palynological samples were taken (modified after Néraudeau et al., 2012, fig. 1).

Fig. 2. Schematic representation of a verrucate spore showing seven out of ten variables measured to run a PCA. S: maximum diameter; SA, LA: smallest and largest value of the reflex, acute or obtuse angle formed by the two tangents of the starting and arrival points of the arc or curve formed by the outline of the interradial region of a spore; miD: minimum distance from the centre to the edge of the spore (excluding the verrucae); maD: maximum distance from the centre to the edge of the spore (excluding the verrucae); DV: diameter of verrucae on one spore; HV: height of verrucae on one spore; ET: exine thickness.

Fig. 3. Species list of palynomorphs recovered from sedimentological units An2–An4 at Angeac.

Fig. 4. Palynomorphs recovered from Angeac sedimentological units An2–An4. Accompanying data are palynological preparation and slide numbers followed by England Finder coordinates. Authors of taxa not otherwise cited in the text are not listed in the references. Scale bar represents 10 µm. **A**. *Abietineaepollenites* sp.; LEM4-1, E23.4. **B**. *Callialasporites dampieri* (Balme, 1957) Dev, 1961; LEM4-2, R53.0. **C**, **D**. *Classopollis torosus* (Reissinger, 1950) Couper, 1958; QPR3669-2; V20.4, K47.3. **E**. *Vitreisporites pallidus* (Reissinger) Nilsson, 1958; QPR3669-3, S35.3. **F**. *Podocarpidites ellipticus* Cookson, 1947; LEM4-2, U31.0. **G**. *Aequitriradites verrucosus* (Cookson et Dettmann, 1958) Cookson et Dettmann, 1961; QPR3669-3, W38.1. **H**. *Cyathidites australis* Couper, 1953; LEM4-1, G52.2. **I**. *Microreticulatisporites* sp. cf. *M. diatretus* Norris, 1969; LEM4-1, X45.0.

J. *Gleicheniidites apilobatus* Brenner, 1963; QPR3669-4, Q20.2. **K**. *Densoisporites microrugulatus* Brenner, 1963; LEM4-1, H30.4. **L**. cf. *Foraminisporis wonthaggiensis* (Cookson et Dettmann, 1958) Dettmann, 1963; LEM4-1, E30.2. **M**. *Cicatricosisporites hallei* Delcourt et Sprumont, 1955 *sensu* Burger, 1966; LEM3-2, G39.4. **N.** *Ovoidites spriggi* (Cookson et Dettmann, 1959) Zippi, 1998; LEM3-2, L34.4. **O**. *Retitriletes* sp.; LEM3-2, D33.2. **P**. *Pilosisporites trichopapillosus* (Thiergart, 1949) Delcourt et Sprumont, 1955; QPR3669-3, V31.2.

Fig. 5. Species of *Concavissimisporites* recovered from Angeac sedimentological units An2–An4. Accompanying data are palynological preparation and slide numbers followed by England Finder coordinates. Authors of taxa not otherwise cited in the text are not listed in the references. Scale bar represents 10 µm. **A**, **B**. *Concavissimisporites apiverrucatus* (Couper, 1958) Döring, 1965; LEM4-1, D33.1; QPR3669-2, E24.1. **C**, **D**. *Concavissimisporites exquisitus* Singh, 1971; QPR3669-3, O27.4, G36.3. **E**. *Concavissimisporites* sp. cf. *C. exquisitus* Singh, 1971; LEM2-1, R40.2. **F–H**. *Concavissimisporites ferniensis* (Pocock, 1970) Fensome, 1987; QPR3669-2, M53.4, N20.4; LEM2-3, C33.0. **I**. *Concavissimisporites robustus* Dörhöfer, 1977; LEM2-3, R34.0. **J**, **K**, **M**. *Concavissimisporites montuosus* (Döring, 1964) Fensome, 1987; QPR3669-2, W31.0; LEM1-1, Q49.0; QPR3669-2, T28.1. **L**, **N**. *Concavissimisporites* sp. cf. *C. crassatus* (Delcourt et Sprumont, 1955) Delcourt, Dettmann et Hughes, 1963; LEM1-1, Q35.4, B28.4.

Fig. 6. Species of *Concavissimisporites* and *Trilobosporites* recovered from Angeac sedimentological units An2–An4. Accompanying data are palynological preparation and slide numbers followed by England Finder coordinates. Authors of taxa not otherwise cited in the text are not listed in the references. Scale bar represents 10 µm. **A**, **B**. *Concavissimisporites*

verrucosus (Delcourt et Sprumont, 1955) Delcourt, Dettmann et Hughes, 1963; QPR3669-3, E20.1, V23.0. **C**. *Concavissimisporites* sp. cf. *C. verrucosus* (Delcourt et Sprumont, 1955) Delcourt, Dettmann et Hughes, 1963; QPR3669-3, D20.4. **D**. *Concavissimisporites uralensis* (Bolkhovitina, 1961) Fensome, 1987; LEM1-1, Y42.3. **E–G**. *Trilobosporites aornatus* Döring, 1965; LEM2-1, S32.1; LEM3-2, B32.0; LEM1-1, K28.3. **H**. *Trilobosporites canadensis* Pocock, 1962; LEM1-1, A28.2. **I**. *Trilobosporites aequiverrucosus* Dörhöfer, 1977; QPR3669-3, S30.0.

Fig. 7. Palynological composition of Lower Cretaceous sedimentological units An2–An4 at Angeac: 250 specimens were counted for each sample except for that from the boundary between An4 and An5, which yielded only 94 specimens.

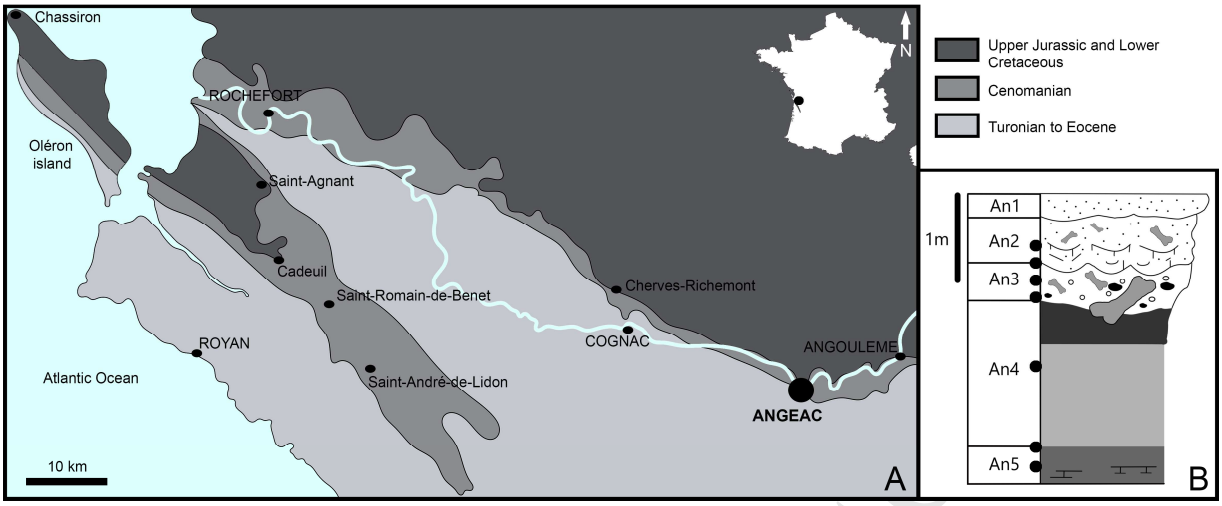
Fig. 8. PCA1 plot of PC1 vs. PC2, with 76.2 % of the total variance extracted, showing the distribution of specimens according to their occurrence in the sedimentological units. For explanation of abbreviations, see caption to Fig. 2.

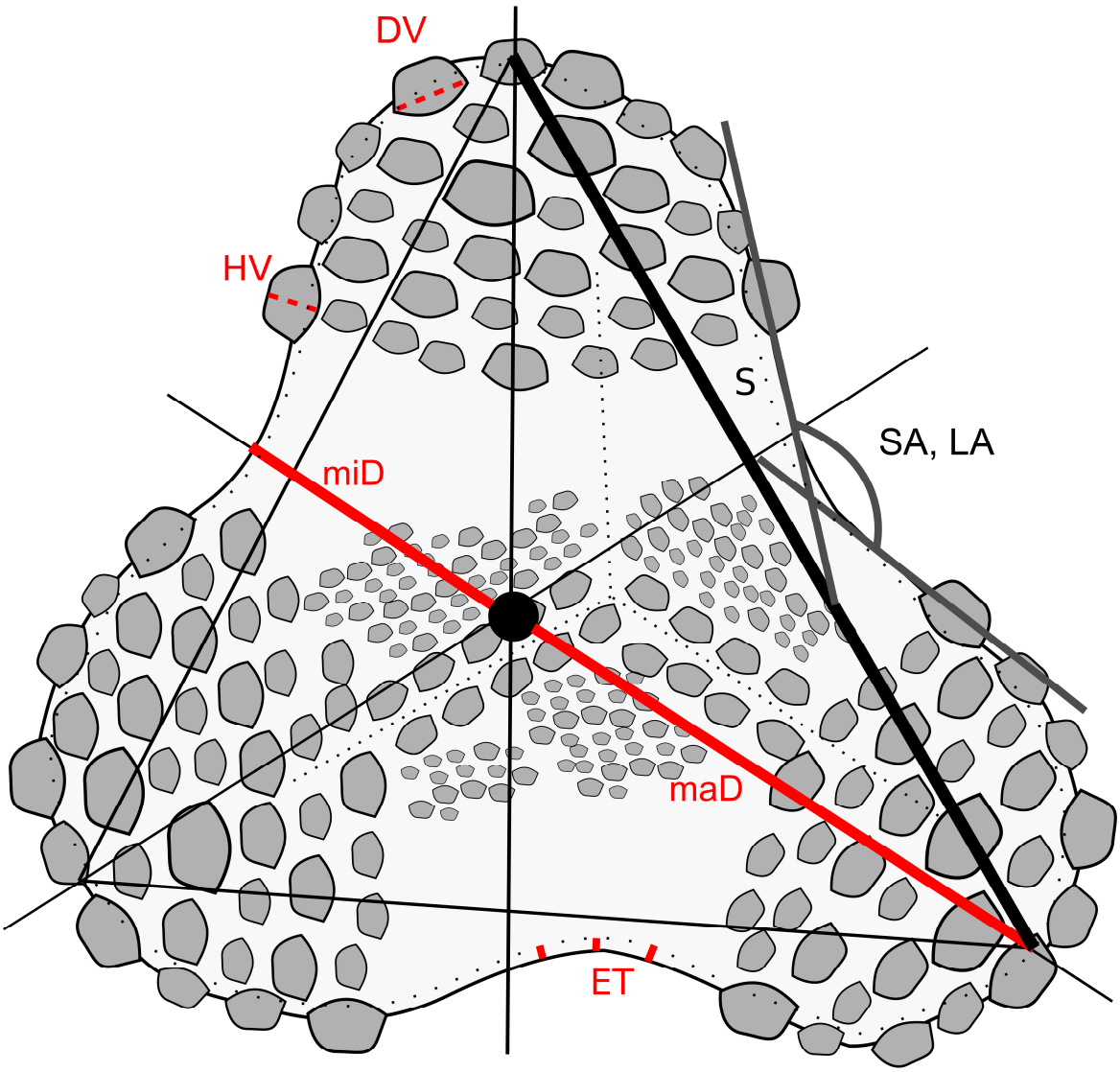
Fig. 9. PCA2 plot of PC1 vs. PC2, with 76.2 % of the total variance extracted, showing clusters corresponding to species of *Concavissimisporites* and *Trilobosporites*. For explanation of abbreviations, see caption to Fig. 2.

Fig. 10. Megaspores from Angeac. **A–D**. *Erlansonisporites* sp. from unit An4, mesofossil preparation MFP512, SEM stub DJB2014/18, specimen 23, IGR-PAL-5780. **A**. Whole specimen. **B**. Close-up of part of triradiate flange and adjacent reticulate wall. **C**. Detail of part of reticulate sculpture showing the structure of the outermost part of the protective wall: the surface consists of a network of sporopollenin threads, beneath which is an irregular,

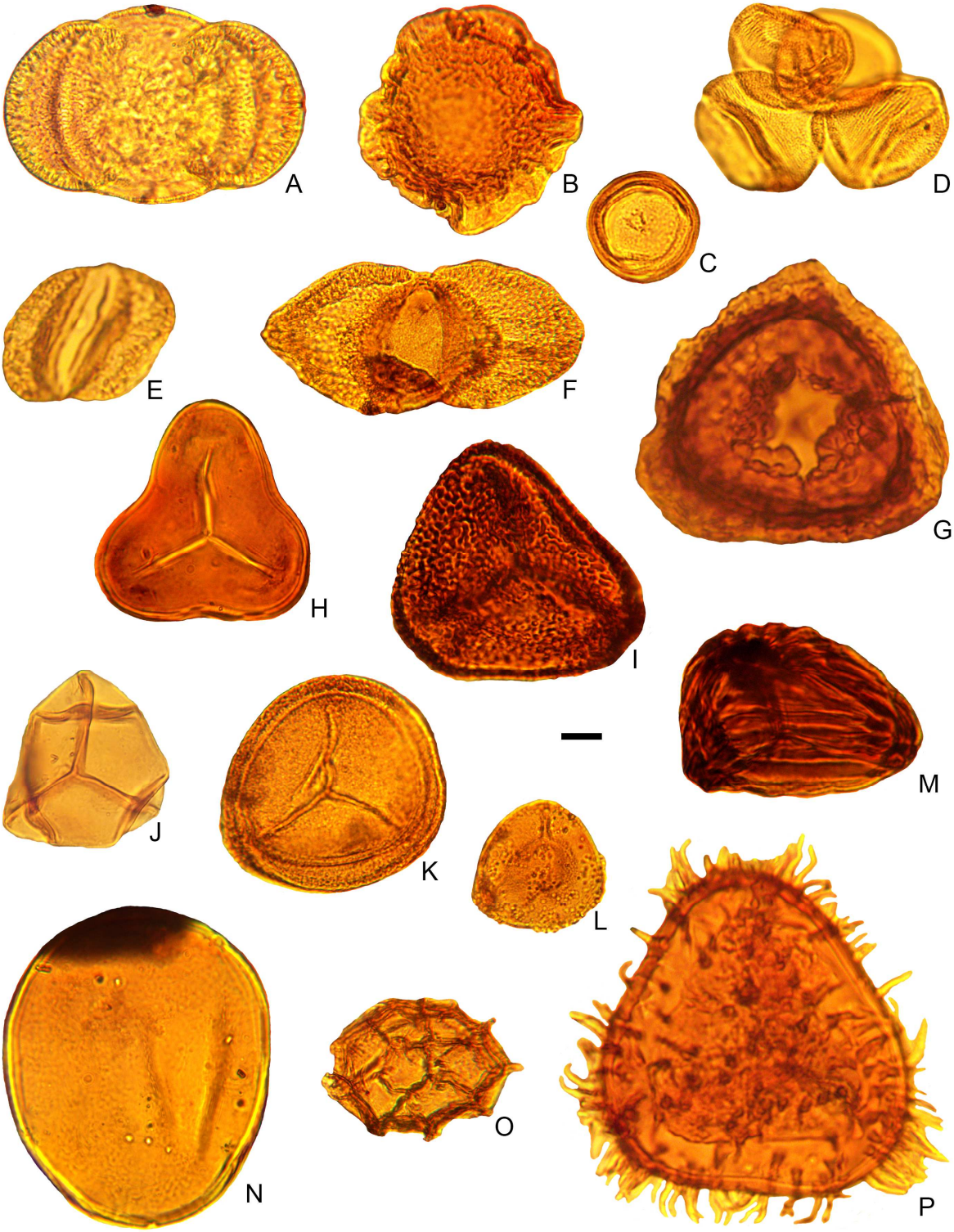
perforated layer. **D**. The same at higher magnification. **E**, **F**. *Erlansonisporites* sp., cf. *Erlansonisporites* sp. in Batten (1975, pl. 13, fig. 6). Mesofossil preparation MFP422, from the boundary between An3 and An4, SEM stub DJB2014/20, specimen 1, IGR-PAL-5781. **E**. whole specimen. **F**. Close-up of reticulate sculpture. Scale bars: A, E: 200 µm; B: 50 µm; C: 10 µm; D: 5 µm; F: 20 µm.

Fig. 11. Megaspores from Angeac, all from mesofossil preparation MFP422, from the boundary between An3 and An4, SEM stub DJB2014/20, specimens 4 (IGR-PAL-5784), 2 (IGR-PAL-5782) and 3 (IGR-PAL-5783), respectively. **A**, **B.** *Erlansonisporites* sp., cf. *Erlansonisporites* sp. in Batten (1975, pl. 13, fig. 6). **A**. Whole specimen in lateral view. **B**. Close-up of a small part of the reticulate sculpture showing microspores lodged within the muri of the reticulum. **C**, **D**. Specimen tentatively identified as *Minerisporites* sp., an atypical representative of this genus (see discussion in text). **C**. Whole specimen in polar view. **D**. Close-up of perforated surface. **E**, **F**. Another example. **E**. Specimen in lateral view. **F**. Close-up of undulating distal surface just below equatorial flange (zona). Scale bars: A, C, E: 200 µm; B, D, F: 20 µm.





	An2	An3	An3/4	An4	An4/5	An5
Abietineaepollenites sp.		°				
Aequitriradites verrucosus		°	°	°	°	
Araucariacites australis	°					
Callialasporites dampieri			°			
Cerebropollenites mesozoicus				°		
Cicatricosisporites hallei sensu Burger, 1966		°				
Cicatricosisporites sp. cf. *C. sternum sensu* Burger, 1966		°		°		
Classopollis torosus		°	°	°	°	°
Concavissimisporites apiverrucatus	°		°	°	°	
Concavissimisporites exquisitus	°	°	°	°	°	
Concavissimisporites ferniensis	°	°	°	°		
Concavissimisporites montuosus	°	°	°	°	°	
Concavissimisporites robustus	°	°				
Concavissimisporites sp. cf. *C. crassatus*	°					
Concavissimisporites sp. cf. *C. exquisitus*	°	°		°		
Concavissimisporites sp. cf. *C. montuosus*	°	°				
Concavissimisporites sp. cf. *C. robustus*	°					
Concavissimisporites uralensis	°			°		
Concavissimisporites verrucosus		°		°	°	
Cyathidites australis			°	°		
Cyathidites sp.	°	°	°	°	°	
Deltoidospora sp.	°	°	°	°	°	
Densoisporites microrugulatus			°	°	°	
cf. *Foraminisporis wonthaggiensis*			°			
Gleicheniidites apilobatus	°			°	°	
Microreticulatisporites sp. cf. *M. diatretus*			°			
Ovoidites spriggi		°				
Ovoidites sp.	°	°			°	
Pilosisporites trichopapillosus	°	°	°	°	°	
Podocarpidites ellipticus			°			
Retitriletes austroclavatidites		°			°	
Retitriletes sp.				°		
Trilobosporites aequiverrucosus				°		
Trilobosporites aornatus	°	°		°	°	
Trilobosporites canadensis	°	°	°	°	°	
Trilobosporites sp. cf. *T. aornatus*	°					
Vitreisporites pallidus				°		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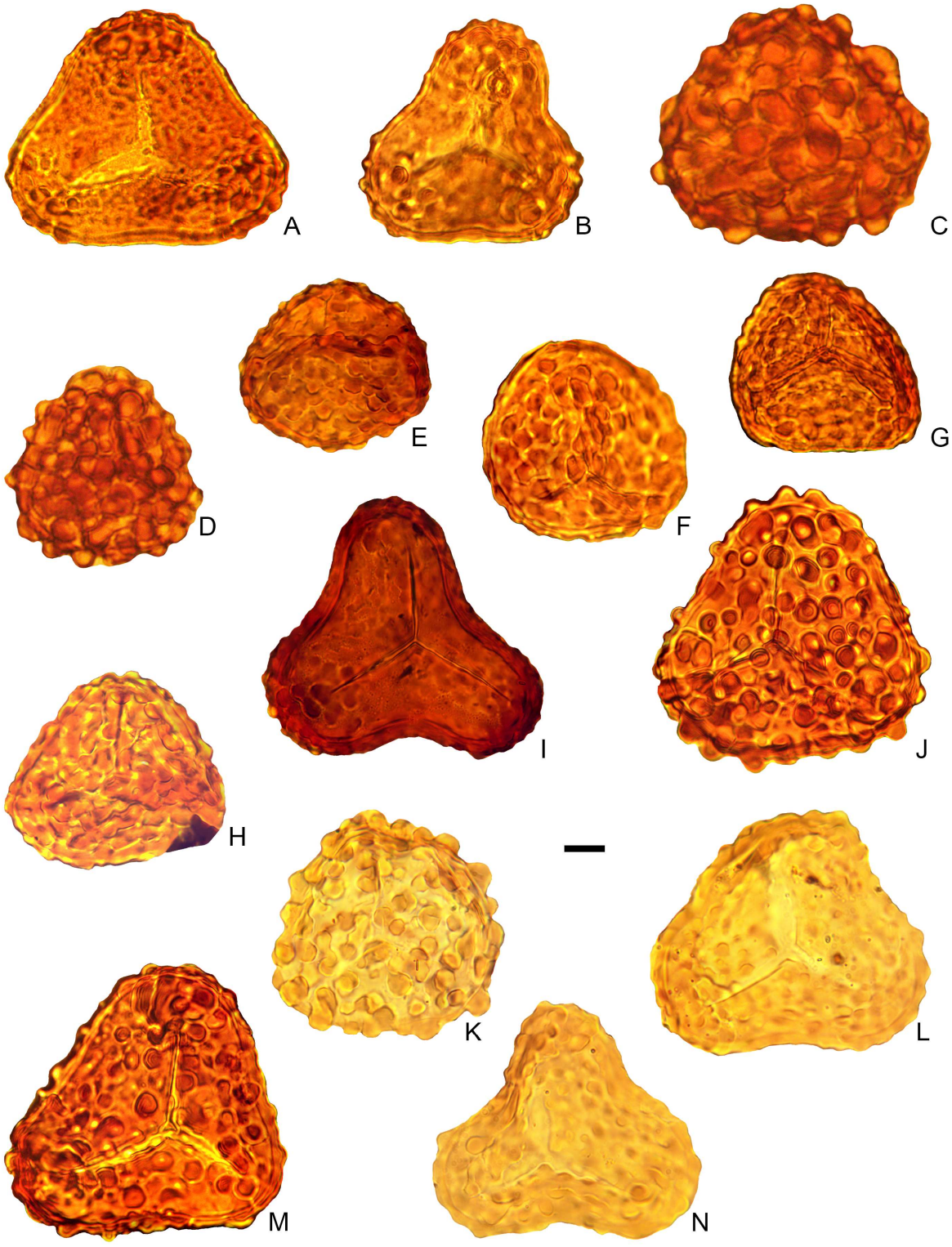
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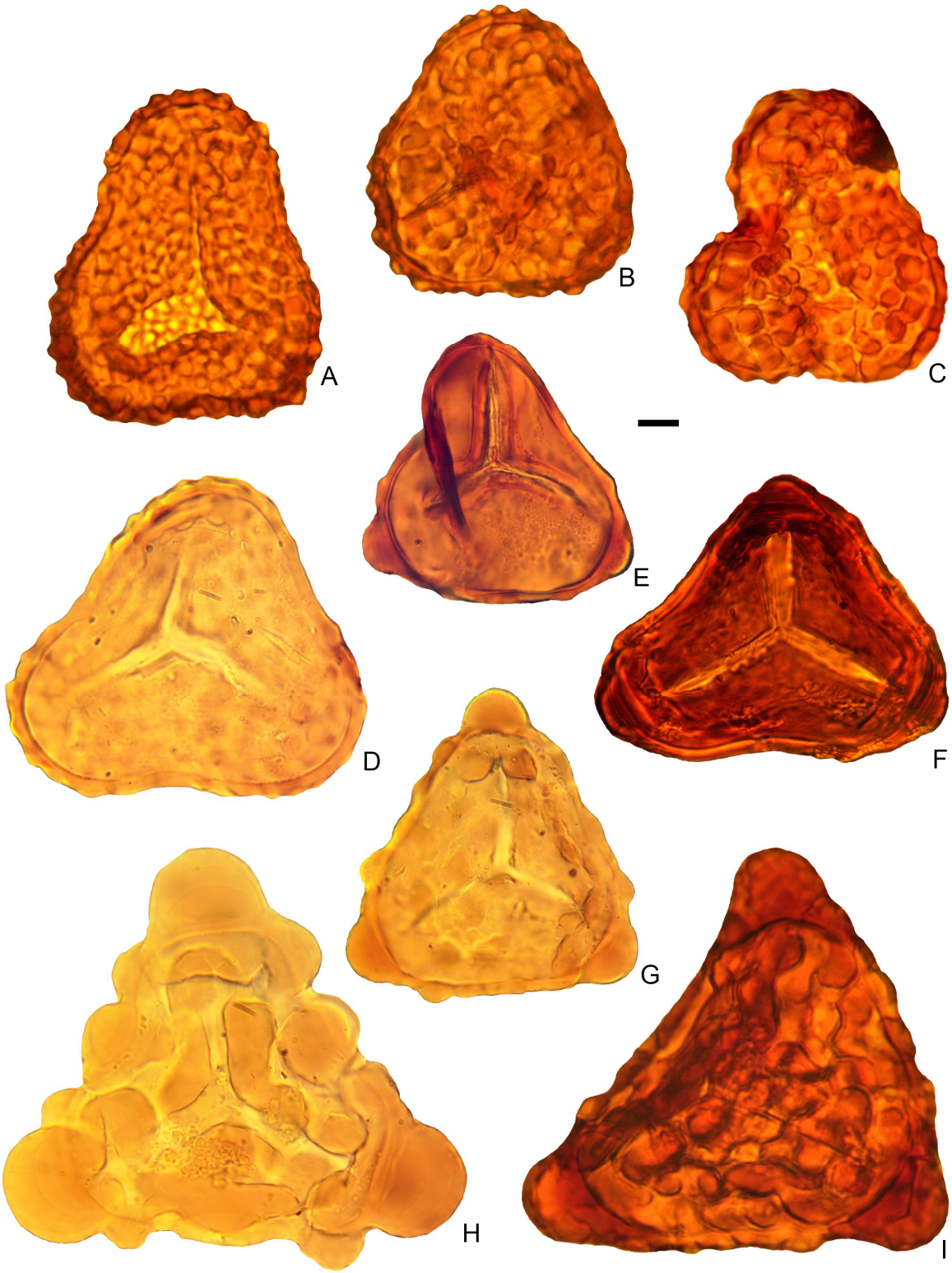
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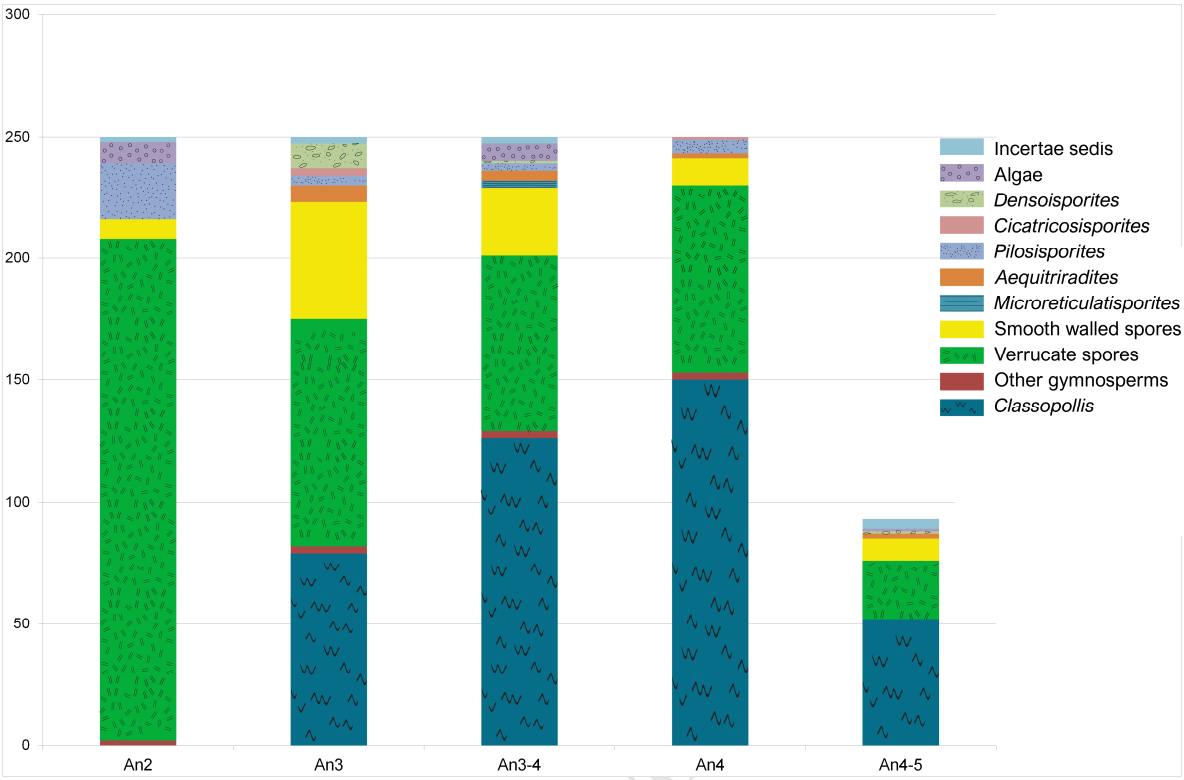

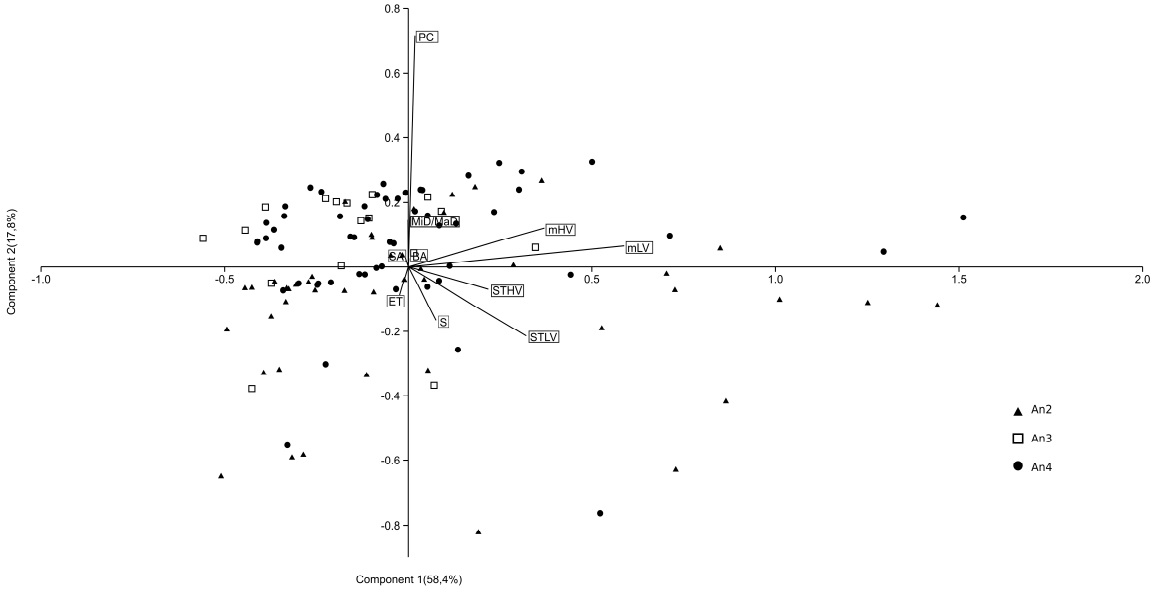

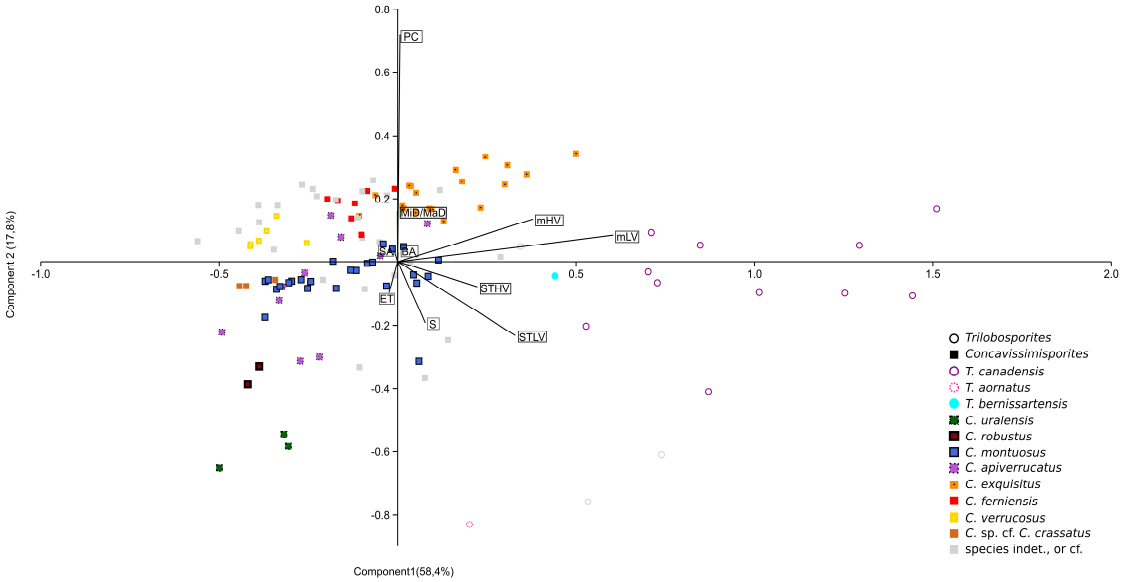

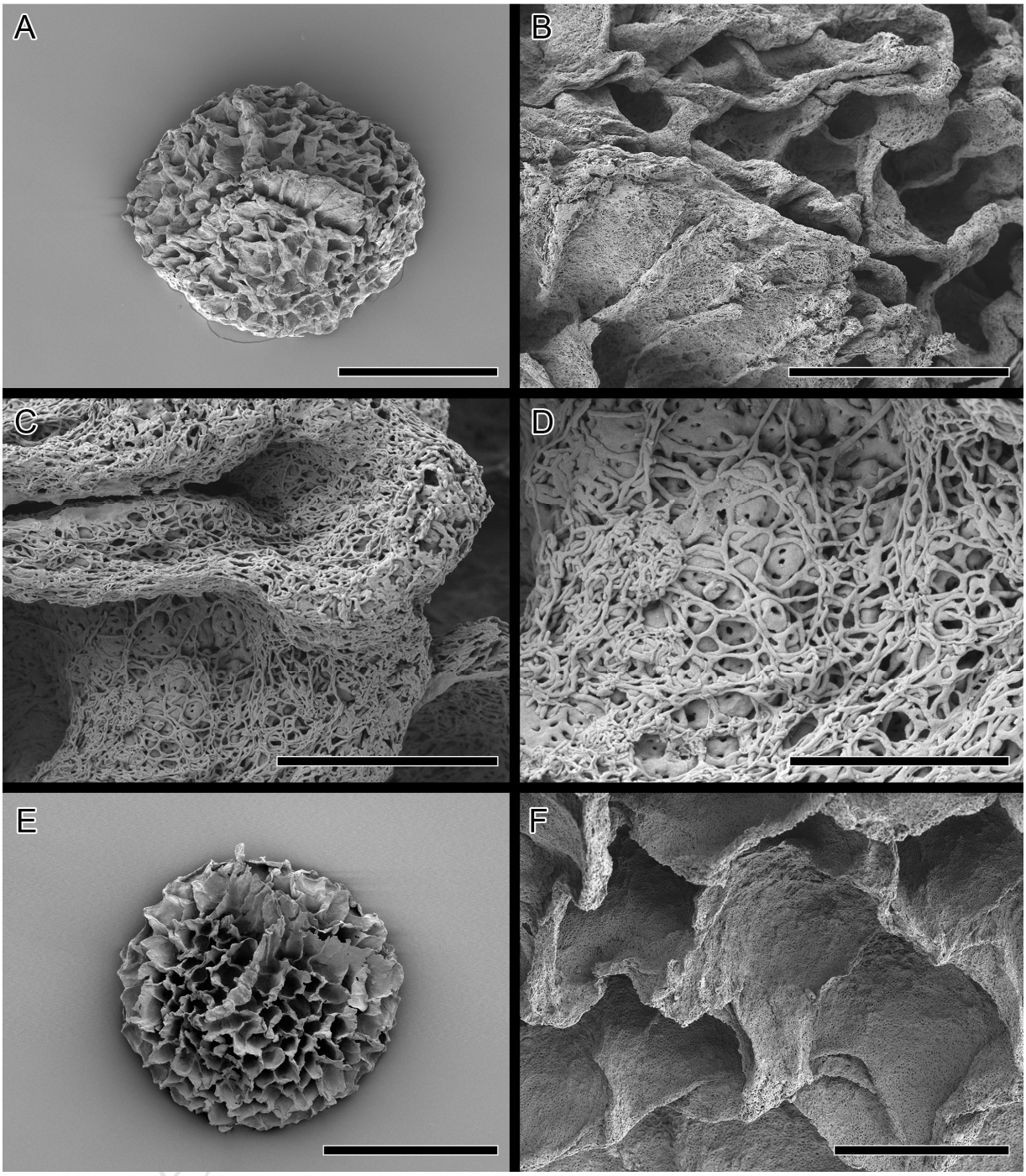
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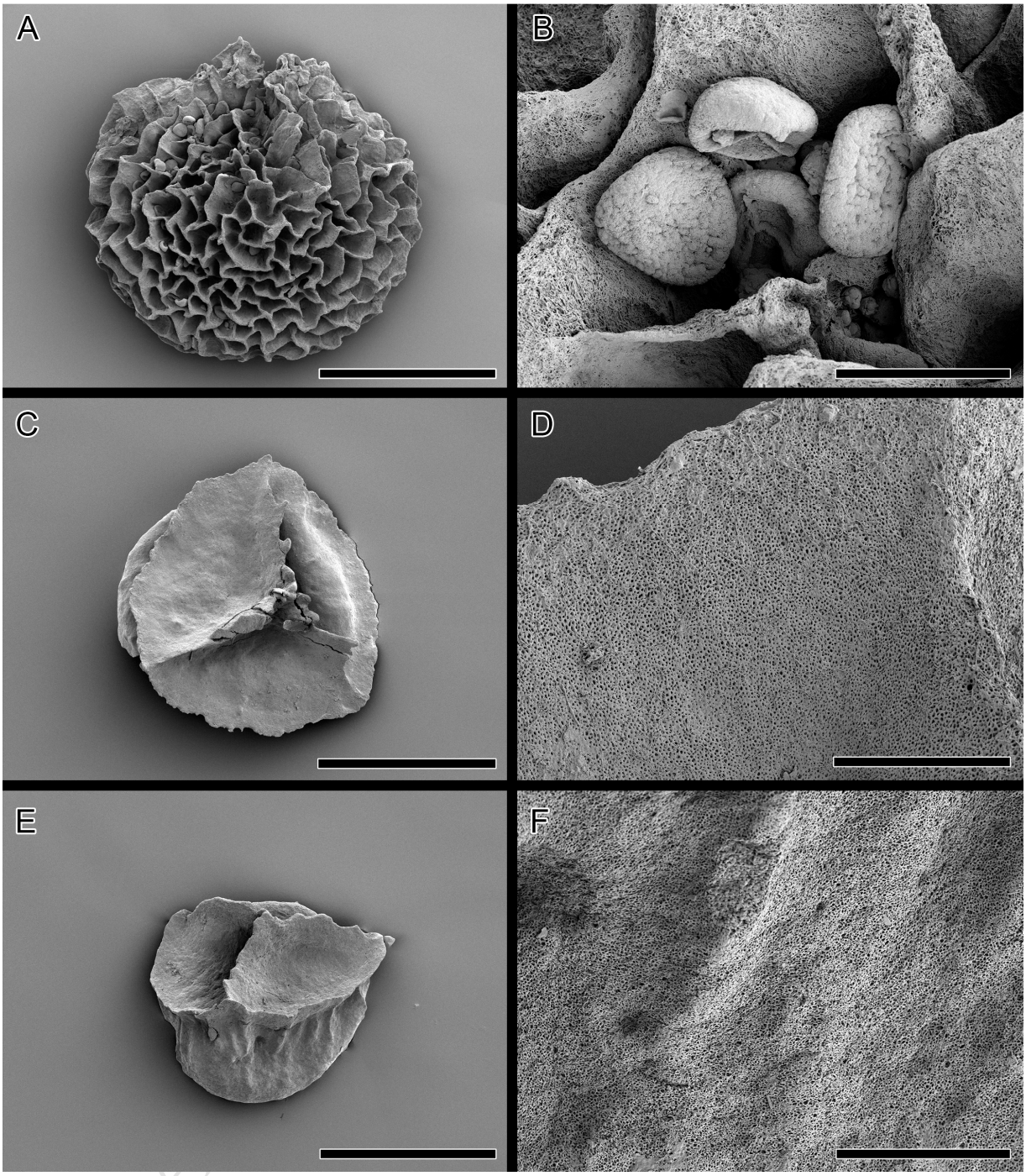
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Highlights

Revision of the palynology of Lower Cretaceous strata at Angeac, western France

Deposition is considered to have occurred during the Berriasian–Valanginian

Eight species of verrucate spores were recovered from the non-marine deposits

All are referred to either *Concavissimisporites* or *Trilobosporites*

The taxonomy and biological relevance of the verrucate spores are discussed